

THE SEARCH FOR AN EVOLUTIONARY PHILOSOPHY OF MAN

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When J. B. S. Haldane suggested that Darwin may have stirred the greatest philosophical revolution of all time, he was voicing a sentiment destined to gain widening acceptance. G. G. Simpson (1964) described Darwin's book, *On the Origin of Species*, as the most important one of the past few centuries because it changed man's attitude toward himself. In a classic discussion of man's biological nature, Simpson (1966) noted:

The question 'What is man?' is probably the most profound that can be asked by man. It has always been central to any system of philosophy or of theology. We know that it was being asked by the most learned humans 2000 years ago, and it is just possible that it was being asked by the most brilliant australopithecines 2 million years ago. The point I want to make now is that all attempts to answer that question before 1859 are worthless and that we will be better off if we ignore them completely.

These may seem harsh words, but their appropriateness becomes more apparent, not less, as one explores the early philosophical literature in light of what has been learned since 1859. Simpson went on to explain his meaning: that whatever we may think or believe about man must be consistent with what we know about evolution and man's history. Prior to 1859 there simply was no general explanation of life, including man, that made any real sense or was consistent with the growing body of knowledge.

Because of its all-encompassing character, evolutionary theory is by nature philosophical in its application to man. But, as Simpson and others have also pointed out, Darwin himself is not generally considered a philosopher. In this apparent contradiction lies part of the reason that I and many other evolutionary zoologists, who may seem little qualified to discuss the question 'What is man?' or to argue philosophy, feel obliged to enter the discussions on these topics. The technological explosion and the population explosion have suddenly removed such considerations from the academic ivory tower; indeed they have forced

man to the brink of a revolution in his view of himself which, if he survives to see it through, will surely overshadow any that has gone before. Overpopulation and war have emerged as global problems, no longer just the problems of this or that nation or this or that society. Simultaneously, they have become the personal problems of every individual with sufficient comprehension to be concerned about his own future and that of his children and his grandchildren. Men are seeking general explanations of human behaviour, and for the first time in history there is real and widespread anxiety in the search. 'What is man?' and what we do with the fragments of answers that we are able to gather are no longer simply the most profound questions facing man, but the most practical and urgent ones as well. My belief in this urgency is the first reason for my selecting the title that I did for this lecture.

The second reason has to do with the history of evolutionary thought. During the first 70 years following Darwin, the concept of the gene, and of the particulate nature of heredity, was incorporated into evolutionary theory. Otherwise, religion and evolution fought a rather dull battle, waves of anthropomorphism followed waves of anti-anthropomorphism, determinism was repeatedly linked with blind induction and so alternately fell into and out of favour; and, perhaps, little else of particular importance to our present topic actually happened.

During the next 40 years, however, evolutionary biology came to life, beginning with the publication in 1930 of Fisher's *The Genetical Theory of Natural Selection* and following through syntheses on selection by Haldane (1932), Sheppard (1958), and others; on speciation and reproductive isolation by Dobzhansky (1937) and Mayr (1942); and on evolution in general by Simpson (1950, 1964) and others.

It has taken a while for the new information and ideas to filter down. In the late 1940s, when

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I was a student taking courses in philosophy, psychology, and biology, none of them had anything to do with the others: evolution was never mentioned in the philosophy course, and only as a nasty word in the psychology courses; behaviour was scarcely mentioned in the biology courses, least of all in connection with evolution, for which flesh and bones seemed the only candidates.

Something quite different is true today. Evolution is finally being recognized by the everyday biologists as their guiding principle, as the thread of continuity, the liaison amongst all of the different kinds of investigations of living materials. Increasingly, biologists are aware that each of them is testing, clarifying, or expanding some aspect of the theory that all features of life have resulted from the evolutionary process as we understand it today. Evolution has become the topic of the first lecture in introductory biology as well as the last; and selection and adaptation are concepts that must be mentioned almost every day in any modern biology course.

If, as I believe, there is no place to seek general explanations of human nature but in the evolutionary process, then we are fortunate that during the past four decades our understanding of this process has grown so immensely. Perhaps—just perhaps—evolutionary biology is ready to meet the challenge that is being thrust upon it.

The third reason for my topic specifically concerns behaviour, which has had perhaps the most erratic history of any aspect of the study of living things. For decades behavioural study was scarcely even respectable in biology, largely because no one knew how to make behavioural observations repeatable and cumulative (therefore 'scientific'), but also because man's behaviour was the last of his characteristics that he wanted placed into an evolutionary context. This reluctance had a considerable effect on the study of animal behaviour. In America, particularly, psychology more or less took over the study of behaviour in the early part of this century, and because of the preoccupation of psychology with man, the comparative and evolutionary aspects all but disappeared and the whole science literally became the study of something called learning. There was no real justification for this, and, perhaps predictably, the concept of learning ultimately came to be used by many as if it were essentially synonymous with epigenesis (or all of the events of ontogeny in which environment and heredity interact). To a degree, the trend is understandable, for the most indirect connections between genotype and phenotype are those between genes and behaviour: behaviour springs

from morphology and physiology, which are by definition, therefore, closer to gene action. For a very long time the last thing anyone thought should be done to understand an animal, not to say man, was to try to relate its behaviour to natural selection and evolution. There was even doubt in some quarters that behaviour evolved!

What had been forgotten was that, while behaviour may be farthest from the genes in terms of how the phenotype (or the animal itself) functions, it is as well closest to selective action. More than anything else, it is the behaviour of an animal that actually causes it to be favoured or disfavoured. If an animal cannot survive subzero temperatures, it may be able to dig a burrow, build a warm nest, or go where temperatures are higher; if food is depleted in one place it can move to another; and so on. In a 'behaving' organism, few aspects of morphology and physiology can be selected except in terms of some intervening or mediating behaviour. One has to wonder why zoologists were so slow to accept that predictability can be increased about even some very subtle aspects of animal behaviour more swiftly by comparing them in terms of life functions, selection, and adaptation than by any other means. I believe there is evidence that our resistance to viewing ourselves and our own behaviour as evolved phenomena has been significantly involved.

The above point perhaps needs illustration (see also Lorenz, 1952, 1966; Lack, 1966; Williams, 1966a; Morris, 1967; Tinbergen, 1968). In some ways we humans are like our domesticated animals because both of us now live in environments so remarkably different from those in which many of our most distinctive characteristics evolved. Although this fact is sometimes used to argue that it is useless to search for the selective action that made man, it can also be used to support the converse argument that we may be able to understand ourselves only by harking back to the nature of our early, different environments.

Anyone who has owned a dog for long will be aware of the propensity of canines for vomiting and re-consuming the results. I am sure that a large number of dog owners look upon this behaviour as some kind of perversion, perhaps deriving somehow from the unnatural environment in which dogs now live. In fact, it has played a vital role in the particular kind of parental behaviour displayed by a variety of wild canines: coming home with a full stomach and regurgitating at the den is the way that canine parents bring food back to their babies in the interim period when the puppies are too large to fare best on milk alone and too young to be taken along on

hunting trips (Scott, 1967; Kleiman, 1967). Vomit is the weaning food of young puppies. With this knowledge we may suddenly acquire reasonable hypotheses about details that might possibly be observed—why one sex might be more likely to vomit than the other, for example, or why a bitch with a litter is likely to vomit near the nest at least once when her puppies are a certain age (I emphasize that these are speculative possibilities based on my own observations and presented for illustrative purposes only; further, there must be numerous aspects of this behaviour, already known to canine biologists, that I am not mentioning).

This sort of insight, which in this case can come only from knowledge of the selective context in which dogs evolved (perhaps now only from studying relatives of dogs), changes our attitude toward dogs and toward this aspect of their behaviour. Many aspects of our own behaviour may similarly seem to be mere perversions, or products of civilization, when in fact they are a great deal older and more complex than this, and perfectly reasonable or understandable in terms of our evolutionary history. Despite many arguments to the contrary (Skinner, 1966; various writers in Montagu, 1968), I believe that the great problems in regard to human behaviour exist because so much of our behaviour, yet today, falls into this category; and I will refer specifically to war, a collective activity that most individuals profess to abhor, and over-reproduction, still being aggravated by the whims of single individuals or pairs of individuals, though feared almost universally by man in general.

The final reason, and perhaps the principal one, for my choice of topic is my feeling that an inexcusably small percentage of the people writing about man today have done their homework on the facts and the theory of evolution. I am not sure why this should be true, but it is disheartening, particularly when one is reading what has been written by eminent and influential people brought together in discussions aimed at solving massive social or political or biological problems. Regarding human behaviour, it sometimes seems that every possible stand has been taken on every possible issue, with no one having any particular reason other than personal opinion for choosing one side or the other. To parade examples can become a lengthy and involved procedure, and I will cite later what I believe to be some of the more important ones. Here I will use a single example, not a particularly critical one, but perhaps instructive, partly because it is not so obvious.

In his recent book, *The Naked Ape*, Desmond

Morris (1967) attempts, with creditable success in some regards, to assist man in thinking of himself as a product of evolution and a relative of other primates. One of his arguments, however, is that breast size and shape in the human female are the results of sexual selection that has run counter to the nursing function of the breast: 'The enlarged female breasts are usually thought of primarily as maternal rather than sexual developments, but there seems to be little evidence of this' (p. 70). Because men like hemispherical breasts, he suggests, they have caused the evolution of breasts that among other things make it difficult for babies to nurse without smothering (p. 106). Morris seems to overlook the point that sexual selection is not really unlike any other kind of selection: thus, if any primitive male's ideas of female beauty corresponded to the kind of breast that was maximally effective in nursing and motherhood, that male would have a reproductive advantage over any of his fellows whose art had less to do with function. This, moreover, is aside from the point that his argument suggests (though it does not require) the unlikely condition of unmated females in primitive societies, since it says nothing about the reproductive advantage of the female whose breasts were more effective in nursing, and who became pregnant rather regularly even though she may not have been considered the belle of the village.

Part of Morris's explanation is evidently inconsistent with evolutionary facts and theory, and the burden of proof is upon him that his original interpretation which supports this portion of his thesis was accurate—that breast shape and size in a general group of humans actually derived their distinctiveness through selection in a direction detrimental with regard to the nursing function. His counter to the 'slight' evidence against his view is apparently his point (p. 70) that 'Other species of primates provide an abundant milk supply for their offspring and yet they fail to develop clearly defined hemispherical breast swellings'. But this seems an inadequate comparison, for several reasons. First, few primates nurse their offspring for the period of several (2-6) years that studies of primitive societies indicate was the case in pre-civilization man—apparently only chimpanzees (Lawick-Goodall, 1968), and probably orangutans and gorillas, approach this condition. Second, he evidently refers to breast size and shape in females that have nursed little or not at all, for numerous published photographs of African, Australian, and Pacific Island women suggest that breasts on mature nursing mothers do not remain spherical and are not as different in shape from those of some other primates as

he seems to indicate. Finally, variations in breast size and shape in very young (or pre-nursing) females, even though not necessarily seeming to correlate with those occurring in mothers who have nursed uninterruptedly for, say two years or more (a difficult situation to discover today in some parts of the world), may nevertheless indicate variations in subsequent potential in the nursing function. Morris's argument may derive from the statement that 'breast size and milk production are not related' (Freedman, 1968) which recurs in the literature. Evidently, it is derived from an examination by Engel (1941) of breasts of 26 British women who died following childbirth. Engel found that some large breasts contained less and lower quality mammary tissue than smaller ones; no information was given on the relative obesity of the women. Engel's sample is small, and there are other data indicating a correlation between breast size and milk production (Maey et al, 1930, 1945). The only demonstration that would really be pertinent to the question raised here is that breast size is not correlated with either amount (or quality) of milk produced or the length of time that adequate quantities of milk could be produced under the conditions (for example, of nutrition for both mother and child) in which the human breast reached its present state. I emphasize that there is no incompatibility between suggestions that breast size (1) correlates (at least roughly) with lactational capability and (2) operates in sexual selection. Nor is it unlikely that large breasts that were inferior to smaller ones in regard to lactation have occasionally been favoured in sexual selection. The problem arises only when the sexual selection is supposed to conflict with the nursing function dramatically and for a long period, and when such selection is supposed to account for the distinctiveness of the human breast.

EVOLUTION: FACTS AND THEORY

Having given at length my reasons for complaining about progress in the search for an evolutionary philosophy of man, I now come to the question: Where does one begin?

Attempts to interpret man's nature in terms of his evolutionary history may utilize insights gained from several different sources: fossil evidence; comparisons involving either man's closer relatives among the primates or other species that have evolved parallel behaviour; comparisons of different populations of men; comparisons of behaviour (or other characteristics) at different ages, and between the sexes at the same ages; and inferences drawn from comparing man against all other forms of life. The last comparison implies that

broadly general or universal aspects of the evolutionary process are involved. This is where I wish to begin. Because of the nature of the disagreements and misconceptions concerning basic aspects of evolution, I believe that it is necessary to establish common ground at the most fundamental level, and that is with acceptance of the fact of organic evolution. By this I mean simply the acceptance (1) that inheritance occurs (like begets like; the reproductive or genetic materials can be passed from generation to generation without change); (2) that mutations occur (the genetic materials do change occasionally, and these changes are in turn transmissible); (3) that selection occurs (all genetic lines do not reproduce equally); and (4) that isolation occurs (all genetic lines are not able, for various extrinsic and intrinsic reasons, to interbreed freely).

All of these four phenomena have been demonstrated repeatedly and can be demonstrated at will, as can their interaction; all of them have been dissected, or are being dissected, in elegant fashions; no living things have been demonstrated to lack any of them or, to my knowledge, are suspected to lack any of them. We have come full circle when biologists such as Muller (1966) and Smith (1966) can conclude that the criterion for life is the potentiality of evolution by natural selection.

If what I have just stated is the essence of the fact of evolution, then, one may ask: What is the theory? In simplified form, the theory is that these component parts, more or less as we understand them today, are sufficient to account for all characteristics of all life: in other words, that everything we see of life about us has been produced by the interaction of heredity, mutation, selection, and isolation. There are ancillary phenomena of great importance, of course—recombination being perhaps the most prominent—but all of these can follow from the interaction of the four more basic features (see also Simpson, 1969).

Acceptance of the above facts means acceptance that man has evolved and is evolving, and leads directly to the hypothesis, using Simpson's (1966) words, that: 'Man owes all his characteristics to their gradual and very slow accumulation because they worked better, because they promoted most successful reproduction and continuance, through all the varying circumstances in which our ancestors lived.'

Perhaps my reasons for beginning at such an elementary level are now apparent: we have passed already to a statement that is probably not a good representation of the working hypothesis of most biologists, not to say the general public.

I think there are two reasons for general failure to accept this hypothesis. First is the persistent notion that evolution is 'only a theory'. The basic facts given above, and the mountains of data supporting them, are still unappreciated by the holders of this view. Second is the recurring suggestion that there are basic flaws in evolutionary theory which excuse us from considering its application to any truly important problem such as understanding man (e.g., Moorhead and Kaplan, 1967; Boulding, 1966). This second kind of disparagement is a much more complex and subtle phenomenon, and I am going to digress for a moment to discuss some examples.

Perhaps the most prominent vehicle of the 'basic flaw' arguments has involved the fact that no one has been able to demonstrate a relationship between (1) which mutations occur in the hereditary materials of the germ cells and (2) which ones will later be saved, or, to say it with teleological implications, which ones will be most useful, or will enable their possessors to outcompete. What this really means is that the causes of mutations (chiefly, at least, radiation) and the causes of selection (Darwin's 'hostile forces' of predators, parasites, diseases, food shortages, and climate) appear to be unrelated: there is no known feedback between them. This is a most important point, for it not only bears on the question of how selection affects mutation rates, but it has been the subject of some confusion regarding the definition of randomness in the direction of mutation. For example, many of the participants in a recent symposium titled *Mathematical Challenges to the Neo-Darwinian Concept of Evolution* (Moorhead and Kaplan, 1967) were evidently operating on the assumption (which seems naive, if only from a chemical point of view) that 'randomness' in connection with gene mutations means that all directions of change are equally likely. Accordingly, among other things it seemed to them that man could not evolve from primeval ooze in the time available. Sewall Wright explained this mistake in his contribution to the meeting, noting that the randomness in gene mutations to which the evolutionists refer is in relation to directions of selection.

It may be instructive to quote two additional authors in this general context. Medawar (1968) has written that our ignorance of the actual mechanics of mutational changes represents a serious deficiency in modern evolutionary theory. No one would deny the very great importance of learning why certain mutations occur and others do not, or why some occur more frequently than others. But, except for the cumulative influence of selection, this is a chemical problem: if the

cause-effect chain is as indirect as seems to be the case, then selection can only save favourable mutations, delete unfavourable ones, and adjust mutation rates as a result of the relative proportions of the two kinds of mutations and the rate of change in the environment. In such case, this area of our ignorance is no more a serious deficiency in *evolutionary theory* than it was a serious deficiency in evolutionary theory a few decades ago to be ignorant of the actual mechanics of heredity while knowing, nevertheless, that faithful reproduction does occur. Again, I do not wish to downplay the very great significance of learning about the nature of DNA, but to place it in perspective. Evolutionary theory could and did pass through many successive stages of refinement solely through knowledge of how accurate reproduction can be, and with total ignorance of its actual mechanics. As we shall see later, this kind of argument may have great relevance to more current problems, such as how to establish appropriate hypotheses regarding predictability and alteration of the course of behavioural ontogeny while still ignorant of cause-effect relationships within the specific ontogenetic process.

Koestler (1967), as still another 'basic flaw' critic, supposed that he had hit upon a remarkable and previously unappreciated 'missing link in orthodox theory' in noting that any genetic innovation undergoes its first test in its effect upon the existing ontogenetic, physiological, and morphological machinery. I am sure that biologists in general will wonder why Koestler thinks this is a new idea; Williams (1966a), for example, gives an excellent review of the hierarchy of environments in which new mutations are tested. All aspects of phenotypes exist solely because the genetic materials responsible proved themselves in past external environments. Because any genetic change may improve any aspect of the phenotype at any ontogenetic stages as well as reduce its fitness or destroy it as Koestler implies, we may also wonder if Koestler himself is quite clear on the significance of the point he is trying to make.

The nature of the 'direction of mutation—direction of selection' link in the cause-effect chain between molecules and organisms may be important for another, somewhat incidental reason: because it marks, perhaps better than anything else, a significant boundary between biology and chemistry. King and Jukes (1969), for example, are probably working about as close as one can get to this boundary from the chemical side when they investigate the largest molecular changes in the genetic materials that are selectively neutral because they are chemically 'synonymous'.

These several examples may seem peripheral to

my topic, but they have previously been used, purposely or more or less inadvertently, to cast doubt upon the adequacy of evolutionary theory. There is an important difference, often overlooked, between criticisms that identify areas of ignorance in the various levels of refinement or detailing of the process of evolution and those which suggest that some serious and basic flaw exists in the general theory. I do not believe that any recent argument in the later category has been successful.

As a final point, it is important to understand that there is no known feedback relationship between mutations and effectiveness in reproductive competition because this fact, together with the dramatic effects of simply altering directions of selection (particularly upon domestic animals) reveals that natural selection is the predominant guiding force in evolution. It is almost entirely upon selection that one must focus his attention if he wishes to trace or understand a particular pathway in the course of evolution, such as that leading to man.

NATURAL SELECTION AND REPRODUCTIVE COMPETITION

Natural selection, or differential reproduction, inevitably implies competition of one sort or another. Before considering different kinds of competition and their relative importance, it may be appropriate to set the stage by describing one of the chief problems concerning the effects of selection upon humans.

Characteristics described as uniquely or most decidedly human are likely to be related to behaviour, and, accordingly, to the complexity of the functioning of man's remarkable and relatively huge brain. Brain size increases correlate across various time levels with fossil evidence of increasing complexity of social organization and the appearance of various cultural phenomena. In spite of arguments based on variability in modern man's brain size, there can be little doubt that the increases in cranial capacity, which can be traced from australopithecine to modern man, are directly related to the increases in complexity of brain function that have resulted in modern man being so different from other living primates (Washburn, 1959; Caspari, 1963; Holloway, 1966; Rensch, 1968; Lancaster, 1968). Crude as it may be, this is still one of our best indices as to when, and how fast, man became a man.

In my opinion, there are three especially interesting questions regarding evolutionary changes in the size of man's brain:

1. How could man's brain increase in size so rapidly from australopithecine to modern man?

In 50,000 to 150,000 generations, or roughly the span of two million years, the volume of the brain case tripled, going from around 500 cubic centimetres to around 1,500 cubic centimetres.

2. What caused the increase in brain size and (particularly) the complexity of its function to go so far beyond that of all other primates?

3. Did the brain stop increasing in size some 50,000 to 100,000 years ago, as is frequently supposed, and, if so, why?

The last of these questions rests upon the skimpiest sort of evidence, namely that the fossils of Neanderthal and Cro-Magnon men suggest that their brains were at least as large as ours are today (Vallois, 1962). Of course they may not have been as complex, but this does not entirely erase the question of why the size increase (apparently) ceased. Evidence from some quarters has suggested that intellectual capacity is not increasing in modern man, and may even be decreasing; other reports, however, indicate that the opposite is more likely (Reed, 1965). Clear evidence of differing rates of change or reversals of direction at any time level, of course, would make any unusually rapid or long-term unidirectional changes all the more intriguing.

An assertion commonly heard in this context, that the pelvis of the human female reached a limit relative to increases in the head size of infants, seems either to stem from a naive view of evolution or to beg the question. Selection always involves compromises of conflicting advantages and disadvantages, and it is difficult to argue that any particular feature of the phenotype has actually reached an absolute physical limit. I am unaware of reasons for supposing that further broadening of the pelvic opening, or other morphologic and ontogenetic changes permitting larger brains, are beyond the realm of possibility if the behavioural situation had continued to favour them. Furthermore, there is probably enough variability among modern women in this regard to discredit the argument that an upper limit of any sort has been reached.

The second of the above questions regarding changes in brain size, which seems to have received the least attention, is in some ways the most interesting of the three. Why is man so different from his closest relatives? Implicit are one or two additional questions: (1) Why has man not speciated? Or: (2) Why have his closest relatives become extinct? I am not so concerned with the first question as with the point that, in the case of rapid evolutionary change of interest here, the second question applies whether or not the extinguished close relatives were members of the same species.

Regardless of the indirectness of the relationship between man's genotype and those aspects of his phenotype that we generally refer to as 'intellect', what we know of the history of changes in man's brain size and in the complexity of his behaviour leads us to the tentative conclusions (1) that variations in intellect were subjected to unusually intense selective action, (2) that this selection was consistent across long periods, and (3) that it carried man's intellectual capabilities right up to their present condition.

There are data of another sort to support this idea. Erlenmeyer-Kimling and Jarvik (1963) have noted that if all of the available data on intelligence test scores are compared, matching individuals of all possible relationships from identical twins to essentially unrelated individuals, and correcting so far as possible for environmental effects using test scores of related individuals, including identical twins reared together and apart, the results are what would be expected if (1) there exists a strong residual of test score differences owing to genetic differences and (2) multiple genes are involved in an additive fashion. These results can scarcely fail to reinforce the idea that generalized increases in intelligence were favoured rather consistently across a long period in man's history. Such a case is just the sort in which one expects the relationship between genotype and phenotype to become increasingly direct, and the accumulation of numerous genes affecting the character in question.

Now let us consider in more detail the ways that natural selection operates. Selection is differential reproduction of alternative genes, or alleles, within populations. It is brought about by differential mortality and differential fertility induced by predators, parasites, diseases, food shortages, and climate. As I see it, there are four possible kinds of such intraspecific competition:

1. Differential reproduction without direct interaction or confrontation between competitors.
2. Partial or complete exclusion of competitors from the best (or only) sources of food, mates, and shelter through aggressiveness and territoriality.
3. Elimination of competitors or potential competitors by killing them.
4. Cannibalism, or the elimination of competitors with food being obtained without additional risk or energy expenditure.

There is an argument for combining the last two forms of competition, but I do not intend to refer to accidental or incidental cannibalism, and the difference between aggression that functions solely in eliminating competition and aggression

that functions chiefly, or partly, in food-getting seems sufficiently fundamental to warrant listing them separately. Furthermore, there will be a greater difference in reproductive potential, on the average, between a well-fed cannibal and his former competitor than between a not so well fed non-cannibal and the competitor he has just killed. I am using the word 'function' here in the sense of Williams (1966a) to mean 'evolved function'—that is, to refer to the probable context of selection, and as opposed to incidental effects.

I emphasize that the focus here is on reproductive competition. Confusion and disagreement about competition (cf. Milne, 1961) may partly stem from failure, particularly by ecologists, to recognize that other aspects of competition are, in one sense or another, secondary or tertiary to this one; and, as Williams points out, it is difficult to see how any organism can escape reproductive competition of one sort or another.

It must be quite clear that the questions of which of the above kinds of competition were involved in man's evolution, which were predominant, and what were the sizes and compositions of the units among which different kinds of competition operated are critical in man's attempts to understand himself. To take what may seem an extreme example, there is no great likelihood that a species in which the chief method of competition has involved only indirect interaction among competitors for 100,000 generations will closely resemble in its behaviour a species in which cannibalism and war have been predominant for as long. Yet just this amount of difference occurs between some of the existing views of man's history.

The different forms of reproductive competition are not equally prevalent in all species, or in all situations in the same species, and the last three, at least, involve different intensities or directness of selective effect. The first, differential reproduction without direct interaction, probably occurs in every species of organism, whether or not the others also occur. This is what is happening when my neighbour has five children and I have two, and neither my neighbour nor I do anything to influence the other's family size or its success. I suspect that this kind of interaction predominates chiefly among simple organisms and in cases in which the influence of Darwin's hostile forces is minimal. One must be careful about interpreting the apparently peaceful interaction of such as my neighbour and me, for, among other things, we may be conspiring—or behaving as though we are conspiring—against some groups external to our neighbourhood.

(I am reminded that someone told Freud about

people living on islands in the South Pacific where the climate was benevolent, food was plentiful, and there were apparently no significant predators, parasites, or diseases, and then remarked that as a consequence these people lived in complete and peaceful bliss. Freud said that he found the last part difficult to believe, and in this particular case he was right. As Captain Cook and a good many others would testify, some peoples living under such seemingly idyllic conditions have formed the most ferocious, war-waging, cannibalistic societies known on earth.)

The second form of competition—exclusion of competitors from food, mates, or shelter through aggression or territoriality—is widespread among animals with complex behaviour (such as vertebrates, arthropods, and cephalopods), and it may be universal among such organisms when commodities are in short supply.

Evidently, in animals with sufficiently complex behaviour, increasing population densities and accompanying shortages of commodities will cause shifts toward the more direct forms of competition. In animals able to predict and plan on a grand scale (man), furthermore, one would expect action to be taken before commodities have actually been exhausted, or before differential reproduction or development of power differentials operate in their disfavour. In all likelihood, we need not fear starvation on a global scale nearly so much as we need to fear the reactions of powerful segments of society to such an impending condition.

The most direct forms of competition, killing of conspecifics and cannibalism, seem rarely to have been observed among animals in general, and it is usually difficult to obtain evidence whether observed cases represent evolved functions or incidental effects resulting from some other kind of selective action—a most important distinction. Reports on cannibalism are not abundant for most kinds of animals; yet man's fossil record is usually interpreted as indicating that some amount of cannibalism occurred more or less continually all through his history at least as far back as the australopithecines (Dart, 1948; Blanc, 1962; Freeman, 1964).

I find it difficult, for two reasons, to be confident about what has been said in much of the anthropological literature tending to diminish the extent and significance of cannibalism. Some investigators (although few of those writing today) have seemed to avoid discussing its prevalence, as if it were a subject best forgotten, and most still use its ceremonial nature to cover the question of function. Ceremonies or rituals associated with cannibalism or any other aspect of human

behaviour may have their chief significance in the encouragement and guiding of an activity functional in some quite different context. It may be easier for a mother to feed her newborn baby to an older child during famine if a ceremony emphasizes the value of this practice to the older child; or, on the other hand, it may be easier to keep the practice of eating newborn infants from growing outside this role and thereby incurring a reproductive disadvantage. It may be easier to keep cannibalism outside one's group if ceremonies keep it related strictly to war and the defeat of one's enemy. In either case there may be reproductive value in either the nutritional or the aggressive aspects of the practice, or both. Even a false belief in the value of eating an enemy's brain, as a further example, could possibly assist cannibalistic groups in destroying and thus out-competing non-cannibalistic groups regardless whether genetic differences in this or other regards exist between them.

Part of the problem is in interpreting the general relationship of cultural change and genetic change. A cultural practice may reinforce, thwart, or not affect a reproductively advantageous behaviour. On the average, however, those features of culture which either reinforce reproductive advantages or replace them with greater ones will outlast those which do not. This is what Simpson (1964) meant when he said (p. 99) that '... culture in general is biological adaptation and ... ethnologists could resolve some of their squabbles and find the common theoretical basis that eludes them if they would just study culture from this point of view'.

All aspects of the phenotype, after all, whether physiological, morphological, or behavioural, are susceptible to alteration and improvement by the specifics of the developmental environment; and all such flexibility is a result of genetic selection. Culture differs from other aspects of behaviour in this regard in being both communicable and cumulative among individual organisms. As behaviour is, in this sense, less directly genetic than morphology and physiology, so is cultural behaviour less directly genetic than behaviour as a whole; but it is not independent of genetic change and natural selection.

At the risk of repetition I must say something here that is basic to my argument. Some investigators caution against possible errors in interpreting evolutionary history almost to the point of rejecting every effort as fruitless. It is possible so to interpret Rappaport (In: de Reuck and Knight, 1966, especially pp. 40-41). Clearly man is not nearly so simple as to be understood solely in terms of added intellectual capacity. But in what

terms? If in terms to be gleaned solely from immediate contingencies or his present situation (cf. Skinner, 1966; Thompson, 1969), why do we continue to be perplexed and helpless in the face of persistence of aspects of man's individual and collective behaviour abhorred by nearly everyone, particularly, perhaps, by parents and teachers who seem to be in the best position to alter them?

Questions of the sort posed in the preceding paragraphs can ultimately be answered. Each such answer cannot fail to have massive effects upon man's view of himself, effects that would be difficult if not impossible to achieve in any other fashion. The more complex man is, the more appropriate is this entire argument. Evolutionists are often accused of oversimplifying man, and they often do: I accuse those social scientists who believe man can be adequately understood without taking full account of his evolutionary history of the same error.

INSTINCT AND LEARNING

As Gilula and Daniels (1969) and Berkowitz (1969) point out, the current search for general explanations of human behaviour (or for explanations of widespread, apparently uncontrollable or undesirable behaviour) has led to a repolarization of opinions that does not differ greatly from that prevalent decades or even centuries ago. Without exaggerating very much, we may call these two positions the 'everything is learned' theory (e.g., most writers in Montagu, 1968) and the 'ineradicable instinct' theory (e.g., Lorenz, 1952, 1966; Ardrey, 1966). It is not surprising that worldwide problems in human behaviour should produce support for singular or unitary explanations such as that they stem from 'ineradicable instincts'. Nor is it surprising that the same idea acquires support from persons who realize that they personally lack any notion of how they acquired tendencies or desires to do certain things, and from persons at least dimly aware that the plunge toward world disaster seems to have been affected little by conscious efforts of mankind despite the armies of social scientists who have been preoccupied with learning theory for the past several decades.

Proponents of the 'everything is learned' hypothesis insist that supporters of the contrary view are also looking for an explanation which relieves them of personal responsibility for their actions; and in somewhat less rational fashion they have even argued that, in any case, their opponents are helping people searching for such excuses. It is hardly reasonable to accuse a man of being a social darwinist because he argues for certain causes of historical events, unless the

appellation has nothing to do with his views of what is desirable for the present and the future of man. It is even less reasonable to imply that he must not analyze human behaviour if his analysis—right or wrong—can be distorted or misused by others. Yet all of these arguments can be found, mixed in with more appropriate ones, in the essays edited by Montagu (1968). One is reminded that the whole idea of man having evolved was cast into disrepute because Hitler distorted it; and it was cast into disrepute for the followers of Karl Marx on an entirely different basis because he distorted it.

It is true that the 'ineradicable instinct' theory seems to call for an entirely different course of action from the 'everything is learned' theory. In the first case we may think of sublimating or substituting; in the second of simply eliminating the appropriate learning situation. But is it really so simple? What does 'everything is learned' really mean? First, we might note that some learning situations are conscious, and perhaps extensively recallable, while others may be completely non-conscious or at least non-recallable. Superimposed on this variation there are differences in the likelihood of occurrence of learning situations that will lead to particular kinds of behaviour. If 'everything is learned', then we must suppose that widespread or universal behaviours are produced from widespread or universal learning situations. The problems are to identify them and, if the behaviour is deemed undesirable, to eliminate them from man's environment. But we seem as yet unable to eliminate whatever circumstances bring about aggression and over-reproduction. At least, we have not been able to do it on purpose, and we have not been able to describe an environment in which we can be reasonably certain that all men could live together without aggression and without overcrowding.

It is not theoretically incompatible with any version of learning theory that some learning situations may themselves be ineradicable, or very difficult to eradicate, from the human environment. I suspect that most biologists accused of supporting the 'ineradicable instinct' theory would settle for having their views interpreted as support for 'ineradicable learning situations'. Whether or not even this is a reasonable hypothesis, it is clear that many different kinds of ontogenetic influences of behaviour occur, that some occur more often than others, and that genetically different organisms respond differently to similar learning situations. Different organisms learn different things, or learn the same thing more or less easily or quickly. To the extent that learning situations leading to aggression or over-reproduction are

difficult to eliminate from the human environment, it may be most practical—or even essential—to think, at least temporarily, in some terms other than those of merely adjusting the developmental environment so as to eliminate the acquiring of aggressive tendencies.

Supporters of the 'ineradicable instinct' theory have been guilty on occasion of making their decision on the basis of what are commonly called 'isolation' or 'deprivation' experiments. One rears a bird, for example, in total silence, even deafening it. If the bird later sings normally, its song is said to be 'innate' or 'inherited', and it presumably enters or approaches the category of ineradicable instinct. But such experiments can never tell what actually leads to the behaviour: they can only reveal that certain stimuli are not involved, or at least not necessary. Of course, the stimuli selected for exclusion are those the investigator has reason to believe are most likely involved in producing the behaviour; one can only say that in those cases in which the behaviour is not influenced by the deprivation, the investigator's ideas in this regard were incorrect, and some as yet unidentified sequence of stimuli was responsible for the behaviour. Deprivation experiments have not identified two fundamentally different kinds of behaviour; rather, they suggest that, in terms of developmental basis, there are several not so fundamentally different kinds of behaviour. They have also exposed unsuspected complexities in behavioural development. It is unfortunate that ethologists chose to deal with behaviours discovered to have cryptic developmental bases by simply labelling them all 'instinctive': and it is even more unfortunate that psychologists in general chose to interpret such labelling as an argument for developmental simplicity or obviousness. Part of the reason for this may be that cryptically developed behaviour typifies many organisms that we consider to be relatively simple. I believe that man's behaviour as a whole has a more complex developmental and neurophysiological basis than that of any other animal; but I also believe that some of its most prominent and influential aspects may have cryptic developmental bases as do some of those behaviours labelled 'innate' in other animals. Some of these behaviours will be difficult to understand developmentally and, at the least, extremely difficult to eliminate universally or on a wide scale.

Unlike Montagu (1968, p. xiii), I believe that all behaviour involves both heredity and environment. Several writers have emphasized recently that when one speaks of any trait as being 'inherited', the remark is sensible only if one is actually speaking of differences in phenotypic

expressions: traits, as we use the term, are actually differences. It may seem at first that many differences in phenotypes, particularly in organisms as flexible as man, are independent of heredity. If, however, two persons decide to learn to play the lute at the same time, it is unlikely that identical teaching and practice will have identical effects regardless of previous experience. With some knowledge of family musical aptitudes, one could probably predict more often than not which way the difference would lie, even if the subjects had been adopted away from their musical or non-musical families at birth. This would indicate that heredity was involved, and not so subtly or indirectly after all, in behavioural differences brought about by instruction and practice in each case. Genotypic identity is rare in humans and, as Dobzhansky (1964) has put it, 'Heredity is particulate, but development is unitary. Everything in the organism is the result of the interactions of all genes, subject to the environment to which they are exposed.' This observation, or hypothesis, suggests that different loci do not act independently in the organism, so that in fact heredity cannot be totally eliminated as a variable in any given circumstance by considering only one or a few loci.

There are some kinds of behaviour in which either heredity is more involved or the instructing and practising experiences are more universal, or both. World problems resulting from human behaviour will frequently involve behaviour falling into these categories because they concern widespread or universal aspects of behaviour. To the extent that this is so, it is not naive to seek general explanations with even relatively low predictive value; the more universal the behaviour, the more significant is an explanation with a particular level of predictive value.

Because heredity and environment are two phenomena, each of which influences behaviour, they are the sources of most dichotomies in referring to behaviour. It does not follow that there is justification for dividing all behaviour into two or a few types on the basis of development and then insisting that man lacks any of the types (See also Hinde, 1968). It is misleading to say, as some recent writers have, that aggression has been 'trained out' of some group of humans when in fact no one knows precisely why aggression has not been displayed in that group; nor is it proper to refer only to one kind of aggression in such a case and imply that whatever was influential in deleting that one kind of aggression in that one small group necessarily applies in any way to other kinds of aggression or to entire nations or the entire world population.

I do not think it is necessary to solve completely this problem of the developmental basis of potentially dangerous behaviours of man before some predictions can be made and some courses of action taken that will begin to alleviate our present problems. I think, further, that understanding of general evolutionary theory, together with current information from the social sciences (for example, see Berkowitz, 1969), will automatically improve man's chances of solving his behavioural problems. Such understanding, moreover, is probably prerequisite for effective investigations of the ontogenetic bases for human behaviour.

SELECTION AND ALTRUISM

Now let us return directly to the hypothesis that man is a product of selection; that all of his characteristics accumulated because they best promoted reproduction. Let us see how easy it is to accept this hypothesis for man.

The most basic assumption deriving from this hypothesis concerns what is commonly called altruistic behaviour, or the act of contributing to another's welfare at some net expense, however slight, to one's own well-being—more specifically, contributing to another's chances of reproducing at some expense to one's own chances. Presumably because it seems the most likely path to peaceful co-existence, altruistic behaviour is held up, among men, as being extremely desirable. There are some other possible reasons for its promotion, which I will leave aside for the moment. In any case, it seems to be one of man's fondest ideas about himself that he tends to think of others first.

However, since evolutionary change proceeds as a result of differential reproduction of genetic alternatives within populations, to the extent that man is a product of evolution, we must at least begin with the hypothesis that, like all other organisms, he is reproductively selfish and never, except by accident or error, truly altruistic.

In this hypothesis, he may be expected to love his neighbours only to the extent that they can assist in his own reproduction, preferably at the expense of theirs. He may be expected to behave as if he is free to do, not whatever does not interfere with the freedom of others, but whatever will indeed interfere with the freedom of others without interfering with his own—whatever, in other words, has a better than average chance of bringing net gain, or whatever will bring the largest net gain to himself, his mate and his offspring—especially to his offspring. It should not be the giving, but the ultimate getting that means the most to him.

He should not care a whit for the perpetuation of the species, only for the perpetuation of enough of it to insure the well-being and continuity of his own genetic line.

Of course he may be expected to avoid revealing all such aims as these, whether or not they be conscious aims, for such revelations are themselves likely to reduce his reproductive possibilities, however slightly. (To anyone thinking that my behaviour here runs counter to this hypothesis, since I am concerned about saving man as a species, I refer to my earlier remark that when a problem becomes a world problem it also, unavoidably, becomes a personal problem).

Man, in short, should really have but one 'instinct', and that is the reproductive instinct (which in his case is synonymous not with sex, but with sex, parenthood, and grandparenthood). There should be only functions subsidiary to this one in his makeup, both individually and collectively. Whatever he may consider, furthermore, even if he chooses to give it names like beauty and poetry and art and charity, should have reached their levels and modes of expression as a result of selection that is nothing more nor less than differential reproduction. (J. B. S. Haldane, 1963, said he accepted this hypothesis for most things, but not for the appreciation of melodies, for which he could think of no function whatsoever. He added that he himself was tone deaf.)

Even self-preservation should be subsidiary to reproduction. Men should be more likely to give their lives in defence of their offspring than in any other situation. Indeed, if we wanted to get very precise about it, comparisons of actual cases should show that there is less reluctance to make such sacrifices (1) as dependent offspring become older, and the parents' energy investment in them increases, and (2) as the parents age, and their likelihood of further reproduction decreases. This general kind of hypothesis is being examined for other kinds of parental animals (Lack, 1966, 1968; Williams, 1966b).

Please remember that I am stating hypothesis—but the kind of hypothesis that most biologists would assume, automatically and without question, for any animal other than man. Acceptance of this hypothesis turns the focus upon the avenues through which reproductive gain has usually been realized by humans; upon how much of the species may generally have been necessary to ensure perpetuation of any individual's genetic line; and upon how man's various characteristics have related to reproductive gains.

I do not imply that the kinds of responses being hypothesized here necessarily depend upon conscious consideration, upon predictions, plan-

ning, or anything of the sort. What an extraordinary problem is that of understanding the significance of conscious learning versus non-conscious learning; of how the different levels or kinds of consciousness have been manipulated by selection specifically to include certain aspects of man's behaviour and to exclude others. Semantic and other difficulties notwithstanding, this is my personal idea of the most exciting of all biological problems. The extent to which the interpretations of behavioural scientists have been obfuscated by this problem can scarcely be over-emphasized. Murphy (1957) is an example, and Fox (1967a) gives an excellent review of the problem in his discussion of incest. I think it is a startling revelation that extensive discussions of the problems of understanding consciousness may fail even to mention evolutionary considerations (e.g., Miller, 1942).

Perhaps, by now, you are saying to yourself: But the hypothesis of non-altruism does not adequately describe man's behaviour! Many men truly are selfless! What about the soldier who falls on a grenade and saves his comrades?

I suggested earlier that there are other possible reasons for promoting altruism than mere peaceful co-existence. Any time there is an external 'enemy' that threatens all, whether it be biological or physical, then altruistic behaviour reaches relatively extreme levels. Such circumstances are those in which profitable returns from 'pseudo-altruism' (seemingly altruistic behaviour which actually yields a reproductive gain, on the average) are most likely, and also those in which pseudo-altruism may be expected to 'spark over' most frequently into truly altruistic, reproductively disadvantageous behaviour (which is how I would categorize the behaviour of the soldier above). Tinbergen (1968) has noted that for the Dutch the sea has served the function of an external enemy; winter may have similarly influenced communal aspects of Eskimo behaviour; and other examples could be cited. Freud suggested that the maintenance of communistic societies depends upon the reality of external enemies, and I believe that the behaviour of such societies, apparently involving conscious manufacturing of such enemies in some cases, supports this suggestion.

There is a curious paradox in the idea of conscious attempts to revise the structure of society as a whole toward Utopian ends. Such plans seem inevitably to involve some special and prominent forms of altruism; yet, in the absence of other 'enemies', the success of Utopias, particularly in terms of persistence, seems always related to the extent to which the members have been able to

view, and to continue viewing, all or some large part of the remainder of society as an external force hostile to their system. Perhaps there is no more succinct commentary on the dilemma of man.

Altruism toward one's close associates is probably never promoted more strenuously, or achieved more completely, than during wartime. Wars are conducted between groups of people. Agreement seems universal that man evolved in groups larger than the smallest reproductive units, as I will discuss later, and this enormously complicates the problem of interpreting selective action on man's behaviour. If one cannot survive or reproduce outside a group, or cannot do so as well (and there are no other reasons for living in groups), then acceptance and approval by the group is prerequisite to reproduction, even if such approval is acquired only at great risk. I suggest that such considerations lead to a view of man's apparent altruism slightly different from that currently present. Extreme altruism may not be undesirable in itself, but to the extent that it is a symptom of alliances of violence or desperation, it can scarcely be viewed as a simple concomitant of peaceful co-existence.

If man is truly a product of evolution, then reproductive selfishness is the most basic aspect of the hypothesis with which any serious attempt to understand him must begin. If we were merely to consider that the challenge is to discover whether or not or how far man may deviate from reproductively selfish behaviour, how he may express his behaviour in terms of this requirement, and what aspects of it may exist in the various levels and kinds of consciousness of which man seems capable, then I would suppose that at last we are on the proper course. I do not see how anything less than this can be satisfying, knowing what we do about evolution and man's history.

Two questions arise at this point: First, how does one arrive at the conclusion that all organisms are reproductively selfish, and, second, how does one transfer such an idea, involving genetic change, even as a working hypothesis, to something as developmentally labile as the behaviour of man?

In spite of wide use of the term 'species adaptation' by biologists (some version of it must occur in every biology text!) and in spite of implications that individual organisms possess a great deal of behaviour aimed at assisting the species or the population even at the expense of the individual showing the behaviour, every such case has alternative explanations in keeping with selection theory. Most have now been studied thoroughly enough to show that the non-evolutionary inter-

pretation was faulty, and, even more important, no scheme has yet been advanced by which genetic variations resulting in truly altruistic behaviour can spread through a population (Hamilton, 1963, 1964a & b; Williams, 1966a).

When a genetic variant that is good for the individual is also good for the population or the species, then it may become universal and be called a 'species adaptation' on that account. But the value to the population or species is not a cause of the selective action but an incidental result of it: if a characteristic is good for the individual (in terms of immediate reproductive competition) but bad for the species (in terms of decreasing, or not increasing, the likelihood of indefinitely long survival) it will lead to the species' extinction unless some change in this connection occurs as the gene spreads (Fisher, 1958). If differential extinction of more or less isolated populations of a species causes genetic change sufficiently rapid to more than counterbalance a reverse genetic change within populations owing to differential reproduction of individuals, then the overall direction of change within the species as a whole can be said to result from 'group' selection (Williams, 1966a, discusses this point). But the disadvantage to the populations of the direction taken by selection within them cannot in itself alter that direction (Wright, 1948). Overpopulation, as exemplified by man, is an appropriate example.

REPRODUCTIVE SELFISHNESS AND OVERPOPULATION

Human overpopulation is the most frightening problem in the world today. I find myself viewing it almost as a disease that is spreading across the planet, and one that may yet prove fatal, partly because it is the chief agitator toward use of weapons that can destroy all life. Every other human problem—war, resource depletion, pollution, crime—fluctuates in seriousness with the severity of overpopulation. This problem is so awesome, and its solution necessarily involves attitudes so alien to the ways that humans have always thought and believed and behaved, that until recently people have been as reluctant to discuss it seriously, and to contemplate it, as they are to discuss or contemplate suicide, or the possibility that there is no life after death and all the consequences of such a realization. Never in the enormously long and complex history of life has it been advantageous to restrict one's reproduction.

In recent years, some biologists and popular writers have promoted the suggestion that man is the only animal lacking 'built-in' population

controls (Wynne-Edwards, 1962; Koestler, 1967), and, in one subtle guise or another, this idea has invaded biological thought on a surprisingly broad scale. The argument is that the reason other species do not keep on increasing as man is doing is because the reproductive individuals reduce their output during lean seasons or years in order to prevent overpopulation, mass starvation, and perhaps extinction of the species. Every biologist who suggests that selection directly favours certain population sizes or densities is supporting this argument, and so are nearly all geneticists who define fitness in terms of populations and then discuss it as an adaptation.

What would happen to genes that facilitated such altruistic behaviour in individuals carrying them? Of course they would be outcompeted by alleles permitting or causing greater reproduction leading to greater overpopulation. There is no way that imminence of extinction, even of the entire species, could change this result.

The same fate would befall genes residing in genotypes which simply gave their phenotypes sufficient latitude to behave altruistically on occasion—that is, when and if more conservative alleles were present as competitors. This is the answer to the most general sort of question that can be asked concerning the flexibility of the phenotype in relation to selection. Perhaps no aspect of development is more widely misunderstood in its relation to selection and evolution than this one.

Most of the examples cited to support the kind of altruism connected with overpopulation involve parental animals which reduce the number of young actually produced and are thereby able to bring more offspring to reproductive maturity, and which will fight in the securing and holding of sufficient territory to protect and feed their young. In other words, one is only witnessing a particular form of reproductive selfishness which has the incidental effect of reducing population density at certain times in the life cycle, but tends overall to increase population numbers and thus density. Man's population density is going up not because he alone lacks a built-in population control, but because he keeps reducing the effects of predators, parasites, diseases, food shortages, and climate. One predicts that in any long-lived parental animal, such as man, some abatement of reproduction will result from increasing population densities, or from accompanying phenomena such as various kinds of tension, strife, and hardship. In the absence of conscious considerations (such as apparently only man can indulge), such behaviour must often have yielded greater lifetime reproduction for the individuals showing it.

Perhaps such behaviour is reflected in the birth rate retardation in the USA that has surprised demographers recently. It seems the height of naiveté, however, to suppose, as some biologists and anthropologists do, that this kind of braking action will lead inevitably to populations kept stable at reasonable levels by birth rates that are continually fitted to the lowest attainable mortality rates.

Even in societies in which newborn infants reportedly are cannibalized to sustain older children or the mother (Basedow, 1925; Bates, 1938), the result is almost surely that the parents bring more offspring to reproductive maturity. If, among predacious birds, stronger nestlings kill and eat weaker ones during food shortages (Ingram, 1959), this behaviour could also increase the parents' reproduction. In some ants, the feeding of fertile eggs to developing young is standard behaviour at certain stages of colony development; we may assume that this is a form of cannibalism that is also selectively advantageous. All of these cases are probably examples of the fourth kind of competition described above, and I believe it likely that many additional instances will ultimately be discovered.

Instead of being the only organism lacking a built-in damper on population increase, man is more likely the only one which has evolved a capacity for truly altruistic reproductive behaviour in relation to overpopulation, even though this capacity is just an incidental effect of the selective action that produced it. Theoretically, at least, man could use his ability to predict and to plan consciously to reduce his reproduction and save his species. Whether or not such behaviour occurs in such a way as to be accurately judged altruistic, there seems to be no evidence yet that any man has actually reduced his reproduction for other than selfish reasons.

Perhaps the most important kind of point that I am trying to make is that man may not be able to use such abilities to save himself until he understands them and himself in terms of natural selection. In other words, I suggest that the only effective way for man to discard any part of his evolutionary background that he decides he does not like is by first understanding it thoroughly—by lifting it into his conscious consideration. This argument is slightly but significantly different from those which imply that man ought to find out about his evolutionary history so that he will know what kinds of things he will be unable to accomplish, or unable to change. The latter approach is one that derives from the supposition of an ineradicable aggressive instinct in man.

Suppose we were to proceed as if convinced

that man is, basically and historically, a reproductively selfish organism. Would this affect our strategy against the disastrous overpopulation into which the world is already starting to plunge?

Among the suggestions of recent writers on this topic, three seem reasonable and immediately possible: (1) giving to all people everywhere the means and the right to delay reproduction and to restrict the sizes of their families (religion seems to be the only major barrier), (2) removal of financial or other tangible rewards for increasing one's family size (the problem is how to do so without depriving children), and (3) educating people concerning the current trends in population growth and their probable results (this step, I believe, cannot fail to foster the attitude that large families may bring doom upon the world and are therefore unacceptable). The importance of the third suggestion probably cannot be over-emphasized, though for a reason that may not be obvious. The desire for approval among one's associates is a selfish reason for refraining from having a large family, and an extraordinarily powerful one. Legislation is merely an extreme way of registering disapproval by providing concrete and specific punishments, and, in fact, many writers see no alternative in this case (e.g., Hardin, 1969).

Lengthening of generation time by delaying reproduction ought to be stressed here because its effect on population growth is generally unappreciated (Cole, 1954), and it may represent a less painful way to ease population growth rates than by simply reducing family size (Ehrlich, 1968). Delayed initial reproduction would almost surely reduce births per marriage as well, though the extent of this effect, when it results from induced or compulsory delays in reproduction, would be difficult to predict.

The problem, however, aside from some kind of legal recourse, is not so much in identifying behaviour that will reduce the likelihood of overpopulation, but in getting individual people to do the things that we already know will change the trend. Unlike some others, I see no basis for believing that the population explosion can be affected significantly by appealing to the consciences of individuals in an altruistic sense. At most, not enough individuals can be expected to respond quickly enough to cause an appreciable effect. At this moment in history I doubt that one person in a thousand, or even in a million, limits his reproduction in order to help save the world. There are always more personal—and more selfish—reasons. It is one thing to frown upon one's neighbour's oversize family, or to keep one's family small because of possible embarrassment,

quite another to consider limiting one's brood so that a neighbour will be better able to raise whatever size of family he may already possess. We can scarcely fail to appreciate Ehrlich's (1968) suggestion that the individual who insists that he has a large family simply because he loves children could have expressed that quality better by adopting some of the unloved, already produced children rather than by contributing to the unhappiness of a future, overcrowded world in which children must live.

I believe that better understanding of man's evolutionary background will reinforce the suggestion that effective approaches to overpopulation must depend upon appealing to responses that are basically selfish as far as individuals, or individual pairs of parents, are concerned, and upon responses which may be importantly involved, though not through any conscious efforts of man, in the prominent cases of static (or nearly static) populations in some nations today. Perhaps we will come to view as beneficial in this regard such things as the presence of complex and multiple gradations of opportunities towards aspects of some kind of the 'good life', whose attainment is clearly dependent upon degrees of financial and other achievements inversely related to age of initial reproduction and family size. Potential parents must be convinced that by reproducing early and increasing their family size they are restricting their children's and their own opportunities in significant fashions. Perhaps the relatively minor penalties for having large families in some affluent countries and the absence of significant or attainable rewards in terms of standards of living in some impoverished countries are both contributing to overpopulation. How to provide adequate rewards in countries already in desperate throes of overpopulation may be an extremely difficult problem. No easy solutions to overpopulation have been proposed, however, and some experts believe it is already too late to avert disaster on a world-wide scale.

AGGRESSION

The argument that man is reproductively selfish also carries implications of special importance in interpreting interactions among people, both as individuals and as groups, particularly for that group of interactions generally labelled as aggressive, and therefore for the threat and reality of war.

Because relatively little intraspecific violence is observed among animals in the wild, many investigators have assumed that man's propensities to violence and war are products of civilization. One argument is that they are simply the results of

frustrations and tension—remove these, and the aggression is removed (Russell and Russell, 1968); another suggests that they are 'learned', or result solely from child-rearing practices and other forms of socialization. Still a third argument is that man has an ineradicable aggressive instinct (Lorenz, 1966). Gilula and Daniels (1969) and Berkowitz (1969) discuss all three of these hypotheses in relation to some current problems.

In this connection it has also been stated, quite recently and by some eminent evolutionary zoologists, that, while most or all animals possess built-in restraints against the killing of members of their own species that function in the welfare of the species as a whole, man lacks such built-in, species-preserving restraints, and this explains the rise of aggressiveness in civilized man. In *King Solomon's Ring*, Konrad Lorenz provides the clearest statement of this argument that I have found (pp. 197-198): 'When, in the course of its evolution, a species of animals develops a weapon which may destroy a fellow-member at one blow, then, in order to survive, it must develop, along with the weapon, a social inhibition to prevent a usage which could endanger the existence of the species . . . There is only one being in possession of weapons which do not grow on his body and of whose working plan, therefore, the instincts of his species know nothing and in the usage of which he has no correspondingly adequate inhibition. That being is man.'

One cannot doubt that in species which evolve lethal weapons, inhibitions against unprofitable use of those weapons evolve as well. How could such weapons be used to the detriment of their possessor? Against a mate. Against offspring. When would their use against a reproductive competitor in the same species be detrimental? Only when that competitor will be useful later on, say, to help kill large game or to help defend against predators; when he can be eliminated from competition through a very much lower expenditure of energy, say, by threat alone; and when he too possesses lethal weapons with which he may mortally wound or disable even though himself be ultimately killed in the process.

No animal lives as long with a single mate as do most men (although many are at least as monogamous). No animal keeps its offspring around it and tends them for as long a period as does man, and as has man, apparently, for at least the last two million years. No animal has acquired weaponry even remotely as powerful as thermonuclear bombs and refrained from their usage as long as has man. Again, I believe that Lorenz and other biologists who support his argument are exactly wrong. Not only do animals in

general lack species-preserving inhibitions of aggression, but man, who clearly has the most elaborate and complicated selfish inhibitions to aggression in the animal kingdom, may also possess the ability to use his intellect purposely and directly to preserve his species from the destructiveness of his aggression. Again, it is an incidental effect of selection, and he has not yet demonstrated that he can use it.

A possible reason that observers of animal aggression have been misled is because in many battles between apparently devastatingly armed beasts, little or no damage is done. I believe that careful observation will show that this is often the case because each individual 'knows' (1) not only how to use his weaponry but also precisely how to defend against that of his opponent, and (2) when it is to his advantage not to press the fight further. The worst kind of animal on which to press an attack with a low probability of gain, after all, is one that has lethal weapons; if you kill him but receive a mortal or disabling wound in the process, you are certain to lose rather than gain. Lions and tigers, one of Lorenz's chief examples, seem not different from nations with nuclear weapons in this regard. Writers who have interpreted the small number of actual deaths in warfare between neighbouring tribes, as described, for example, in Matthiessen (1962) among New Guinea peoples, as evidence of some kind of inhibition to killing, miss the point that such outcomes may actually be evidence of closely matched groups, and that the excessive bluffing involved in such warfare may be part of the estimates by each group of the other's strength. If such were the case, then even single killings might be extremely important in shifting the balance, and one might expect that significantly weakened groups would avoid battle and sometimes join forces with other groups even when great risk or sacrifice was involved. Both kinds of behaviour have been reported in primitive societies.

When the weapons of a species are restricted in their versatility, stereotyped responses may effectively prevent damage, and, as a result, one may see what looks like a ritualized or sham battle—even a comically specialized one. Again, I suggest that we are probably always seeing, in such cases, exceedingly well-matched opponents rather than sham battles, and that observers might learn this very quickly if they could be suddenly cast into the skin of one of the combatants and had to dream up their own responses.

Matthews (in Carthy and Ebling, 1964) suggests that chimpanzees are not highly aggressive, as is indicated by the tolerance of the presence of subordinates by the dominant, so long as he

is given first choice of females and food (and, one presumes, sleeping spots!). Assuming that Matthews is correct (however, see Lawick-Goodall, 1968), one wonders what else a dominant chimpanzee might gain from his position. Others have suggested that gorillas, with all their size and strength, are always peaceful, yet Dart (1961) reported a death battle between two dominant males of adjacent bands.

That ritualization and threat can be effective in establishing and maintaining dominance without injuries or death is evidence only that both inhibition of aggression and aggression are subject to natural selection. Aggressive interactions are also crucial when they are conducted by threats: but acceptance of appeasement signals by a dominant can only evolve if it benefits the dominant, just as appeasement, or giving in, can only evolve when, on the average, the subordinate also gains by giving in. As commodities become less and less available, less advantage is realizable from giving up.

In weighing the possibilities of gain or loss in aggression, degrees of desperateness can be involved in extremely complex fashions, just as probabilities more or less directly linked with actual reproduction, as I have suggested above (see Hamilton, 1963, 1964a, b; Laek, 1966; Williams, 1966b), can be 'weighed' in extremely complex fashions.

Complex or all-out appeasement, such as may be the case in exposure of vulnerable regions at close ranges by a subordinate, probably could be successful only if there had been a long history of appeasement (Lorenz's often-quoted example of exposure of the jugular vein region by subordinates is doubted for wolves and dogs on apparently firm grounds by both Schenkel, 1967, and Scott, 1967; evidently, it is the dominant which displays this behaviour). Appeasement may arise from (1) successfully confusing an opponent into a parental or male-female response or (2) gradual reduction and change from minimally effective retreating. Rudimentary appeasement may be no more than departure from the vicinity of the other individual's food, mate, offspring, or territory. A dominant animal might give up the chase early because it will be unprofitable, either because it yields no further gain, and may yield loss if further combat ensues, or because it renders the defended objects or space more vulnerable to other potential usurpers.

By the various arguments I have given, what appears to be or is presumed to be altruistic behaviour should evolve only in one or another, or some combination, of four contexts: (1) care of offspring, (2) care of mate, (3) gaining and

maintenance of approval and status in groups within which one must operate to live and reproduce, and (4) maintenance of such groups. Tolerance or appeasement in aggressive interactions should fit roughly the same pattern.

In keeping with the suggestion that man is reproductively selfish and that all other functions are subsidiary to reproduction, I would argue that if anything approaches being inevitable in him, it is not aggression but the taking of gain. The best hypothesis seems to be that aggression is neither an inevitable instinct, nor solely associated with tension or frustration or overpopulation. It is probably best interpreted as a behaviour that may be expected to occur whenever it is likely to lead to gain that, in terms of man's history, can be translated as having potential reproductive value.

Regardless how pessimistic it may seem at this moment, so far as I can see, the only apparent way to prevent wars is to develop and maintain situations in which each potential participant remains convinced that he cannot gain by war. In this light, one cannot be happy at the prospect of the development of defenses against nuclear weapons, which may be the only reason we have not recently been involved in major wars. This position supports arguments for the urgency of an international peace-keeping agency, and it suggests that an effective one will not be organized until the powerful nations are all convinced it is in their own best interests.

GROUP-LIVING AND WAR

When animals live in groups by necessity, then we ought to expect relative intragroup peacefulness because dominants gain from not hurting subordinates or exiling them from the group. Appeasement, therefore, should be more complex in animals which live in groups.

Perhaps it is importantly related to his evolutionary history of living in groups that modern man seems perplexed because while he is doing what, individually, seems appealing, right, moral, appropriate, reasonable, enjoyable, and peaceful, groups of men nevertheless carry out actions that he, individually, abhors—partly because they seem to endanger him or inconvenience him or his family.

Primitive men lived in co-operative bands, apparently for the past two million years at least; on this point there seems to be no disagreement. Living in groups larger than the smallest reproductive units, however, inevitably involves certain disadvantages. The most important of these seem to be increased competition for all commodities and greater likelihood of disease and parasite

transmission. Why, then, should animals live in groups—that is, groups larger than the smallest reproductive unit, say, a single male and his female or females and their offspring?

I believe that only three reasons can be advanced to explain animals living in tightly knit groups: (1) susceptibility to predation is lowered either because of aggressive group defence, as in savannah baboons, or because of the opportunity of causing some other individual to be more available to predators, as in schooling fish and herds of small ungulates; (2) the nature of prey prevents individuals or families from securing enough food to make splintering off profitable, as in wolves in certain regions; or (3) there is a shortage of space for some essential function, such as breeding sites of some marine birds and mammals. Of course, more than one of these functions may be involved in any particular case of group-living; one suspects that some penguins, for example, might profit both in food location and in escaping from predators by staying in groups as they move about in the ocean, and the clustering of their nests and young may likewise be advantageous both because of predators and because of shortages of nesting sites that are maximally suitable for other reasons.

In any case, in the absence of one or more of these three kinds of advantages, group living has to be detrimental because it reduces the individual's chances of using his own peculiar abilities to out-reproduce his neighbours.

The almost universal explanation for group-living in man is that he profited from hunting game too large for single men to kill easily (Washburn, 1959; Washburn and Jay, 1968; Hockett and Aseher, 1964). The evidence is that fossil tools, weapons, and bones indicate that man has hunted large game for perhaps the past two million years, and that agriculture did not exist on a very broad scale until a few thousand years ago. The general enthusiasm with which modern men hunt, and co-operate in hunting, the tendency of men to group, and the ease with which children learn to hunt and kill game, have also been used as supporting evidence.

This is a most important argument, for, indeed, the adaptive significance of group-hunting is most often given as the selective context in which man became a man, by which his brain size tripled across two million years and he acquired his present intelligence and his other peculiarly human traits. So long as this is true, this idea is the most significant one that can be mentioned regarding man's history. It would seem that nothing could be more important for our understanding of man than the presence of an alternative more likely

than this one. Yet I believe that such an alternative exists.

Essentially the same kinds of evidence as given above indicate that man has been a warring, cannibalistic animal during the same lengthy period—when he was, in fact, becoming a man—and during all agricultural periods as well and even perpetually in regions where group-hunting was never practised and big game was never available and food shortages were unknown. Furthermore, man himself is a more demanding protagonist or prey than any other kind of animal; the selective effect of direct warfare, as I have indicated, would be more direct and a better explanation of very rapid evolutionary change; and war seems to crystallize co-operative efforts more dramatically and effectively than any other human activity. Not only is there no upper limit on effective group sizes in war, as in hunting groups, but there should have been continual pressure to increase group sizes, particularly as technology advanced means of conducting warfare and increased intelligence made massive co-operative effects possible. In contrast, if hunting had remained the chief context of group-living, group size should have gone down with increasingly effective weaponry and predatory strategies.

I suggest that, at an early stage, predators became chiefly responsible for forcing men to live in groups, and that those predators were not other species but larger, stronger groups of men. Once men began to function in groups, even if only to hunt big game at first, there is every reason to suppose that they would have used their collective ability to make it impossible for individual men to reproduce outside groups. This kind of situation has apparently prevailed every time modern men accustomed to living apart with their families in agricultural societies have tried to establish themselves in new lands already peopled with humans living in hunting-gathering bands, or lacking in sufficient population and law to prevent predatory bands from forming and persisting out of their own ranks.

Intraspecific aggression exists on two levels when animals are forced to live and interact in groups. I would speculate that killing and, to a much lesser degree, cannibalism, have for a very long time been man's chief mode of reproductive competition at the inter-group level; and the two kinds of competition that fall short of killing more prevalent within groups. I do not believe that the kind of mild and largely indirect competition central to the hypothesis that man evolved intelligence because it enabled him to hunt better can easily be used to explain the rapid evolutionary change in men living in bands, and least of all

man's divergence so far from his closest living relatives.

To relate and contrast this view to those prominently advanced recently to account for man, I would note that it emphasizes intraspecific rather than interspecific competition (cf. Brown, 1958; Schaffer, 1968). It suggests that the most important 'environmental change' (cf. Robinson, 1963) was the development of culture, not, however, chiefly as a better means of hunting (cf. Dobzhansky and Montagu, 1947; Hockett and Ascher, 1964; Bartholomew and Birdsall, 1953; Washburn, 1959; and most others), but chiefly as a better means of warfare. Finally, it suggests that war was the chief vehicle of intergroup selection, and that intergroup selection was more important, as compared to intragroup selection, than has generally been considered the case. Others, such as Freeman (1964), Emlen (1966), and Ardrey (1966), have already argued that war has played a significant role in human evolution; the particular role suggested here has previously been advocated by Alexander and Tinkle (1968) and Alexander (1969).

One question remains from the three posed earlier concerning explanations for evolutionary changes in man's brain size: Why did the brain apparently stop increasing in size, or the trend even reverse itself, a few thousand generations ago? Assuming for the moment that this is not a false question, to answer it one may ask, first, how selection is apparently affecting brain functions such as variations in intelligence (as measured by scores on intelligence tests) today. The answer, regardless of the present direction of change, must be given not only in terms of intragroup selection—relative family sizes, child mortalities, and percentage of successful marriages (and of, especially, paternity *per se*)—but also in terms of the effects of war or intergroup strife. Except for particular cases in which variations in family size and child mortality might be characteristic of populations that are genetically different in regard to brain function, war seems to have reached a technological stage, and the powerful nations have become so genetically mixed and in many cases alike, that war can scarcely be affecting man's genetic makeup in a very consistent fashion (see also Livingstone, 1967). There are some fairly recent (though small-scale) examples to the contrary, such as total annihilation of the Tasmanian natives by Europeans. In no such case, however, do we have good reasons to believe that significant changes, either way, have been brought about in the brain function of man as a whole.

The situation postulated earlier for primitive man, in which warfare is argued to be chiefly re-

sponsible for increases in brain size, is quite different. It calls for war to be waged in some relationship to degrees of genetic difference and raises the question of the selective value and background of assisting one's closer relatives at the expense of non-relatives or distant relatives. In any species engaging in the more violent kinds of intraspecific competition, ability to recognize and spare close relatives would be highly favoured. Such an effect, moreover, would have been facilitated by man's tendency to live in small bands or family groups. Members of one's own band could automatically be treated as relatives, or tolerated and even assisted; those of other bands could equally automatically be treated as competitors or the enemy. Man is aware, to an extraordinary degree, of differences in his relationship to the other men with whom he lives. In some modern hunting-gathering peoples still living in small groups, and in which intertribal aggression is prevalent, the extent and nature of such knowledge has amazed anthropologists more than any of their other attributes. Part, but perhaps not all, of the value of such knowledge has surely been related to outbreeding; despite continuing denials of this function (Farb, 1968, Livingstone, 1969), the extensive knowledge of genetic relationships and stringent marriage laws that exist in small, isolated groups of highly uniform (and evidently inbred) people such as some Australian aboriginals (Radeliffe-Brown, 1951) strongly support this argument (see also Fox, 1967a). Livingstone uses an evolutionarily unlikely 'group selection' hypothesis of the sort criticized above to support his rejection of a deleterious inbreeding hypothesis for incest. Both he and Farb (and many others) imply that because incest (as a consciously applied rule) is cultural, it cannot be related to a history of genetic selection. Livingstone's argument is that extreme inbreeding was favoured in early hominids because it decreased the frequencies of genes deleterious in the homozygous condition. He admits that such changes would 'take a rather long time in some cases', and (later, in discussing small gorilla bands) that 'even a very small amount of gene flow would counteract this trend toward complete homozygosity...'. The long time required and easy counteracting by outbreeding seriously detract from his argument, for any individuals successfully outbreeding would be favoured by their avoidance of deleterious homozygosity. My arguments in this paper support an hypothesis opposite to his: that long-persisting and essentially universal cultural practices such as incest avoidance are most likely

to be reinforcers of previous trends in genetic selection.

CONCLUDING REMARKS

Approaches to the question 'What is man?' and 'What do we do about it?' include, as I have already indicated, studies of fossils, of primate biology, and of living men. All of these approaches are being pursued more effectively now than ever before, and attempts at synthesis are becoming more frequent and more convincing (Freeman, 1964; Emlen, 1966; Howell, 1967; Fox, 1967b; Lancaster, 1968; Tinbergen, 1968; and many others). General understanding of the evolutionary process influences not only how the results of all investigations of man are interpreted but, probably more importantly, how they are selected and prosecuted in the first place. The potential profoundness of this influence can be appreciated by examining the papers published across the past two decades in any major anthropological journal, such as the *American Anthropologist*.

Nevertheless, we have scarcely begun to examine man in this light, partly because not everyone who is aware of evolution, and willing to accept it, understands it, and partly because only a tiny fragment of the world's population has yet become involved in what I shall term this 'major philosophical revolution'. The list of human activities that deserve to be reviewed and investigated further with this kind of insight is indefinitely long. One could mention the nature of sexual dimorphism and its patterns, in behaviour as well as morphology, throughout life; the significance of menopause; the appropriateness of various attitudes toward pre-marital and extra-marital sex; monogamous and polygamous tendencies in the two sexes and under different conditions; the significance of relationships between revolution-minded youth and the 'power structure' under different conditions of stress and affluence; the genesis and maintenance of inter-group hostilities and war; the nature and significance of genetic variations among the peoples of the world; and educational systems, social systems, penal codes, city planning, and international politics. No activity of man is exempt. Furthermore, it will not do to leave the questions of how man's evolutionary background bears on these problems to a few individuals. Evolution is no longer the property of a small group of biologists: to understand it thoroughly has become the responsibility of every person with a potential role in man's future.

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Robert S. Bigelow's 1969 book, *The Dawn Warriors* (Little-Brown, Boston) was published just before this manuscript was submitted, but I did not learn this until several months later. Although Bigelow and I published together on another topic in 1960, we did not become aware until 1968 of our common interest in the present topic. Our similar arguments were derived independently.

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